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AUTHOR(S):

Hanya, Goro; Bernard, Henry

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Fallback foods of red leaf monkeys (*Presbytis rubicunda*) in Danum Valley, Borneo

Goro Hanya * and Henry Bernard †

* Primate Research Institute, Kyoto University, Inuyama, Japan

† Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Sabah, Malaysia

Correspondence to: G. Hanya: Primate Research Institute, Kyoto University, Kanrin 41-2, Inuyama, Aichi, 484-8506 Japan. E-mail: hanya@pri.kyoto-u.ac.jp, Tel: +81-568-63-0542, Fax: +81-568-63-0564

Running title: Diet of red leaf monkey

Abstract Animals in Southeast Asia must cope with long periods of fruit scarcity of unpredictable duration between irregular mast fruiting events. Long-term data is necessary to examine the effect of mast fruiting on diet, and particularly on the selection of fallback foods during periods of fruit scarcity. No such data is available for colobine monkeys, which may consume substantial amounts of fruits and seeds when available. We studied the diet of red leaf monkeys (*Presbytis rubicunda*, Colobinae) in Danum Valley, Sabah, northern Borneo, using 25 months of behavioral observation, phenology and vegetation surveys and chemical analysis to compare leaves eaten with non-food leaves. The monkeys spent 46% of their feeding time on young leaves, 38% on seeds, 12% on whole fruits, 2.0% on flowers, 1.0% on bark, and 1.2% on pith. They spent more time feeding on seeds and whole fruit when fruit availability was high and fed on young leaves of *Spatholobus macropterus* (liana, Leguminosae) as fallback foods. This species was by far the most important food, constituting 27.9% of the total feeding time, and the feeding time on this species negatively correlated with fruit availability. Consumed leaves contained more protein than non-consumed leaves, and variation in time spent feeding on different leaves was explained by their abundance. These results suggest that red leaf monkeys show essentially the same response to the supra-annual increase in fruit availability as sympatric monogastric primates, increasing their seed and whole-fruit consumption. However, they depended more on young leaves, in particular *Spatholobus macropterus*, as fallback foods during fruit-scarce periods than did gibbons or orangutans. Their selection of fallback food appeared to be due to both nutrition and abundance.

Key words: diet; fallback foods; functional response; general flowering,

Spatholobus macropterus

Introduction

Seasonal environmental changes can impose serious food shortages or physical stress on animals. For example, animals in Southeast Asia must cope with extreme super-annual seasonality in flowering and fruiting. In lowland dipterocarp forests in the Malay Peninsula, Borneo and Sumatra, many plants come into flower simultaneously for a few weeks to a few months and subsequently set fruit massively (mast fruiting); however, these species of plants rarely flower outside these general flowering events (Sakai 2002; Wich and van Schaik 2000). General flowering events occur at unpredictable intervals every 2-6 years (Sakai 2002). Variation also occurs spatially. For example, mast fruiting may occur in only one region, or may occur on the entire Malay Peninsula (Yasuda *et al.* 1999). Between mast fruiting events animals must survive a long flower- or fruit-scarce period of unpredictable duration. The larger inter-annual variability in fruiting in SE Asia than in other regions (van Schaik and Pfannes 2005) is thought to have strong effects on community structure and may be responsible for the low species diversity observed in this region (Reed and Bidner 2004).

Animals in SE Asia cope with this strong seasonality in various ways, including both numerical and functional responses. Numerical response occurs both by migration and reproduction, and thus immediate response is possible for volant and/or fast-reproducing animals, such as giant honey bees (*Apis dorsata*) (Itioka *et al.* 2001) and thrips (Ashton *et al.* 1988). However, a functional response is often the only option for non-volant, slow-reproducing animals. The

order primates is a particularly interesting taxon in this context, since primates are among the few large animals that can use the canopy, where most plant reproduction takes place. Most primates do not increase their number in response to the fluctuations of fruit availability, although orangutans may show resource-tracking migration (Buij *et al.* 2002). Instead primates rely on the resources available in their current habitat, meaning that fallback foods play an indispensable role in their survival in seasonal habitats. The two species of orangutan (*Pongo abelii* and *P. pygmaeus*) offer the best examples of primate functional response to mast fruiting. Their diet consists mostly of fruits during mast fruiting, but they fall-back on young leaves and bark during non-fruiting seasons (Kanamori *et al.* 2010; Knott 1998; Wich *et al.* 2006). Furthermore, orangutans accumulate fat during the mast fruiting period and metabolize it when the fruit availability decreases (Knott 1998). However, data for other species are scant, as long-term data are necessary to reveal the effect of mast fruiting.

Data on non-frugivores are particularly needed to understand the effect of strong super-annual seasonality in fruit abundance on primate populations. Despite the classical view that primates of the subfamily Colobinae are obligate folivores (Clutton-Brock 1977), colobines are now known to consume substantial amounts of fruits and seeds, with the average fruit- and seed-feeding time of 24 colobine species reaching 31% (Kirkpatrick 1999). Although they sometimes feed on fleshy fruits, they typically consume only unripe ones, as acidic fruits may disrupt the forestomach fermenting system (Lambert 1998).

We studied the diet of red leaf monkeys (*Presbytis rubicunda*) in the primary lowland dipterocarp forest of Danum Valley, Sabah, Malaysian Borneo,

for 25 months. Red leaf monkeys can be classified as folivorous/gramnivorous; their feeding time over 13 months at Sepilok, Sabah, was composed of 36% young leaves, 30% seeds, 19% whole fruits, 11% flowers and other minor foods (Davies 1991). We aimed to (1) describe dietary changes of this species in response to seasonal fluctuations in fruit and young leaf availability, (2) identify the fallback foods they feed on during the fruit scarcity, i.e. foods for which consumption was negatively correlated with the availability of preferred foods (Marshall *et al.* 2009), and (3) elucidate the chemical and distributional properties that explain the differences of consumed vs. non-consumed and frequently vs. rarely consumed young leaves.

Methods

Study site

The study site is a primary forest around the Danum Valley Field Centre (4^{O}57'N, 117^{O}48'E, 300 m above sea level) within the Danum Valley Conservation Area (438 km^2) located in eastern Sabah, northern Borneo. During 2007 and 2008, rainfall was 3,115 mm/year and mean daily maximum, minimum and mean temperatures were 31.4^{O}C, 22.5^{O}C and 26.9^{O}C, respectively (Fig. 1; data provided by the Danum Valley Field Centre). The forest is predominantly composed of lowland dipterocarp trees (Newbery *et al.* 1999). Canopy height is approximately 50 m, with emergent trees more than 70 m.

Behavioral observation

We observed one habituated group of red leaf monkeys with 8-12 individuals from around 6:00 until 16:00, 5-10 days per month. We recorded their behavior

by scan sampling: every ten minutes we recorded the activity (feeding, moving, resting) of all visible individuals, except for dependent infants. When they were feeding, we recorded the food category and collected samples for later identification. We collected data for 25 months from December 2006 to December 2008. Total observation time was 1141 hours, and the monthly observation time was 16-87 hours (mean: 46 hours). Observation time per day was 7.22± SD 2.27 hours. Sometimes we could not find monkeys in the early morning or terminated observation before 16:00 due to heavy rain. Therefore, observation time in the periods of 6:00-7:00 (46 h), 14:00-15:00 (88 h), and 15:00-16:00 (79 h) was less than for other hours of the day (104-149 h). However, this bias in observation time is unlikely to have influenced the main results because it was similar across months

Phenology

We used data on monthly tree phenology accumulated by the Danum Valley Field Centre since July 2004, using the same plot set as Norayati (2001) and the same protocol as the census conducted from August 1997 until December 2000 (Wong *et al.* 2005). They monitored flushing, flowering and fruiting activities of 511-533 identified trees of ≥10 cm DBH every month. Plots were situated in primary forest, including the home range of the study group. The monitored area consisted of five transects, each 20 × 100 m, placed every 400 m along the 2 km trail.

Vegetation

We took data on the botanical composition of the forest from Lingenfelder (2005).

The vegetation plot was different from that used to study phenology but covered a larger area. We used data for a 4-ha plot in the study site, for which all trees ≥10 cm DBH were identified to species and their DBH measured. Because these data did not include lianas, we added data on *Spatholobus macropterus* (Leguminosae), an important food source for red leaf monkeys at this site. We set a transect along a circular trail which covers most of the home range (ca 16 ha), of 4 m × 1.2 km and recorded the presence/absence of this liana for all trees along the transect.

Chemical analysis

We compared the chemical properties of young leaves consumed and not consumed by the red leaf monkeys. We sampled young leaves of all species that constituted at least 1% of the feeding time and the top 20 species in abundance (basal area) in the study area of the vegetation survey (Lingenfelder 2005; Newbery *et al.* 1996). We included young leaves of 7 consumed species and 16 non-consumed species in analyses.

For each tree species consumed, we took young leaf samples from at least four individual trees from which the monkeys had been feeding. We sampled at least 20 leaves for each species. We kept the leaves in plastic bags and took them to the Field Centre where we dried them immediately at 60°C for 60 hours using an oven. Afterwards, we stored the leaves in plastic bags and took them to the laboratory at the Primate Research Institute, Kyoto University, where we dried them again at 60°C for 48 hours using a vacuum incubator. After weighing, we milled leaves, put them into a plastic tube and kept them in a desiccator.

We determined crude protein using the Kjeldahl procedure for total nitrogen and multiplying by 6.25. Since fiber-bound nitrogen is not taken into account, metabolizable protein may have been lower (Rothman *et al.* 2008). We measured crude lipid as diethyl-ether extract by the Soxhlet method (Soxhlet 1879). We determined crude ash by ashing at 550°C. We estimated neutral detergent fibre (NDF) following methods in van Soest (1991). We extracted condensed tannin with 50% methanol and determined its presence / absence using the butanol-HCl method (Porter 1989). We used presence / absence since it is difficult to estimate the concentration of condensed tannin with this method (Rautio *et al.* 2007). We used the ratio of weight of the constituents to the total dry weight for analysis of crude protein, crude lipid, NDF and crude ash.

Data analysis

Due to the high canopy and dense vegetation, the number of individuals we observed in each scan was low (mean: 1.95, SD: 1.12). To avoid over-representation of highly visible behaviors or foods, we divided the number of individuals engaged in each activity (in case of feeding, number of individuals feeding on a particular food item) for each scan by the total number of individuals observed in the scan (Agetsuma 1995; Harrison 1985; Maruhashi 1981). We summed this value for each month for each food item and calculated the proportion this represented of the total feeding record. Patterns in the seasonal variations in the diet evaluated with and without this correction were similar, and the results for the effect of phenology on diet did not change.

We examined the effect of the proportion of fruiting and flushing trees in the phenology survey on the proportion of feeding time of the particular food

192 category (or species) using a generalized linear model (GLM). We used data for
193 each month as the unit of analysis (N=25). Since the data were significantly non-
194 normality (Kolmogorov-Smirnov test, $p<0.05$), we applied the quasi family and
195 calculated quasi AIC (Akaike's Information Criterion) using the 'QAIC' function of
196 the package 'MuMIn' in R 2.13.2 (Burnham and Anderson 2002). We combined
197 fruit and seed feeding because we expected these two categories of foods to
198 respond in a similar way to fruit availability. We used only the food species in the
199 phenology census for the analyses, although we also present data on all food
200 species. The variance inflation factor (VIF) was 1.05, which was less than the
201 cut-off value (5), so collinearity among independent factors did not affect the
202 results. We choose the model with the smallest AIC among all possible
203 combinations of independent factors, including the null model.

204 We examined young leaf food selection at two different levels using
205 GLMs. We examined the following six independent factors: crude protein, NDF,
206 crude ash, crude lipid, presence/absence of condensed tannin, and abundance
207 (number of stems/4 ha, using the vegetation data). First, we examined the effect
208 of these properties on whether the monkeys fed on a species (1) or not (0)
209 (binomial distribution). Then we examined the effects on the proportion of
210 feeding time for food leaves. We started from the full model and then decreased
211 the number of independent factors until the AIC did not decrease any further
212 (backward stepwise). The maximum variance inflation factor (VIF) was 2.35,
213 which was less than the cut-off value (5), so collinearity among independent
214 factors did not affect the results.

215 We used R 2.13.2. (© The R Foundation for Statistical Computing) for
216 all the statistical analyses. We set the alpha level at $P<0.05$.

217

218 **Results**

219 Phenology

220 There was one clear peak of fruiting during the 25 month study, from May to
221 October 2007 (Fig. 2a). This was the largest peak in the period August 1997 to
222 December 2000 (Wong *et al.* 2005). During this high fruiting period, 2.8-6.7% of
223 trees bore fruits while only 0-1.9% of trees did so out of this period. The number
224 of flushing trees also fluctuated considerably (Fig. 2b).

225

226 Overall diet

227 Red leaf monkeys fed on young leaves (46% of feeding time), seeds (38%),
228 whole fruits (12%), flowers (2.0%), bark (1.0%), pith (1.2%) and other foods
229 (unspecified foods and mature leaf, 0.2%). The monkeys ate all whole fruits
230 unripe and masticated the seeds. They consumed plant parts from at least 122
231 different species (identified at least to genus level) belonging to 50 different
232 families, 103 of which we identified to species (Table 1). The main food families
233 were Leguminosae (10 species), Lauraceae (10), Euphorbiaceae (8), Meliaceae
234 (8) and Sapindaceae (7). Young leaves of *Spatholobus macropterus*
235 (Leguminosae, liana) were by far the most important foods, which constituted
236 27.9% of the total feeding time, followed by the seeds of *Chionanthus pluriflorus*
237 (Oleaceae, 4.2%) and *Nothaphoebe umbelliflora* (Lauraceae, 4.1%; Table 2).

238

239 Seasonal variation

240 Red leaf monkeys increased seed and fruit consumption and decreased
241 young leaf consumption when fruit availability was high (Fig. 4). The best-fit

model predicting fruit+seed consumption included only a positive effect of the percentage of trees fruiting (Table 2a). The best-fit model predicting young leaf consumption also included only the percentage of trees fruiting but with a negative effect (Table 2b). The percentage of trees flushing was not included in these best-fit models (Fig. 5). The model that included only the percentage of flushing trees was the second-best fit to explain the fruit+seed consumption and young leaf consumption, which had ΔQAIC values (difference from the QAIC of the best-fit model) of 0.40 and 0.33, respectively. The model that included both the percentage of flushing and fruiting trees was the third-best fit, and it had a ΔQAIC value of 1.98, for fruit+seed consumption as well as for young leaf consumption.

When fruit availability decreased red leaf monkeys consumed young leaves of *S. macropterus*. Feeding time on young leaves on *S. macropterus* (27.9%) was much longer than for the second most important leaf species (*Ziziphus angustifolia*, 1.5%, Table 3) and *S. macropterus* was consumed in each of the 25 study months. Feeding time on the young leaves of *S. macropterus* was significantly negatively correlated with the percentage of fruiting trees (N=25, r=-0.49, P=0.012, Pearson's correlation), but the sum of the feeding time of the other species was not (r=-0.27; P=0.17). Feeding time on young leaves of the second- and third-most consumed species, which constituted more than 1% of the total feeding time, also did not correlate with the percentage of fruiting trees (*Xanthophyllum affine*: r=-0.15, P=0.48; *Ziziphus angustifolia*: r=0.06, P=0.77).

Young leaf selection

Red leaf monkeys chose young leaves which contained more crude protein than

leaves of common species as food, and consumed the most abundant species *S. macropterus* most frequently. The best-fit model for the difference between consumed and non-consumed leaves included only a positive effect of crude protein content (Table 4a). The second- and third-best fit models included crude ash or lipid in addition to crude protein, and these had ΔAIC=1.97 or 2.00, respectively. A high protein content increased the likelihood that a leaf species was selected as food. The protein content of young *S. macropterus* leaves was the third highest (20.5%) and 1.5 times higher than the mean value of the 23 species examined (13.8%). The difference between consumed and non-consumed species was not significant for NDF ($t=1.72$, $P=0.10$), crude ash ($t=1.18$, $P=0.25$), crude lipid ($t=1.04$, $P=0.31$), and abundance ($t=0.59$, $P=0.56$), but significant for crude protein ($t=4.78$, $P=0.0001$; Fig. 6).

GLM model selection did not identify the most significant factors explaining the variation in feeding time among food species because the best-fit model included 5 independent factors (Table 4b). The second-best-fit model had an extremely larger value of ΔAIC (28.9). However, we found a significant correlation with feeding time for abundance ($N=7$, $r=0.99$, $P<0.0001$) but not for the other factors (NDF: $r=0.52$, $P=0.23$; crude protein: $r=0.16$, $P=0.72$; crude ash: $r=0.63$, $P=0.12$; crude lipid: $r=0.01$, $P=0.98$). In addition, there was no difference in feeding time between tannin-free and tannin-bound species ($t=1.33$, $P=0.24$). This suggests that the effect of abundance was more important than other factors.

Discussion

Response to fruiting seasonality

Red leaf monkeys increased whole fruit and seed consumption in response to increased fruit availability, and increased young leaf consumption when fruit availability was low. Qualitatively, these findings are essentially the same response as that shown by monogastric Bornean orangutans and Müller's gibbons (*Hylobates muelleri*) (Kanamori *et al.* 2010; Vogel *et al.* 2009), which live sympatrically with red leaf monkeys in various parts of Borneo, and indicate that fruits and seeds are preferred foods for all of these primates. However, the responses of red leaf monkeys and sympatric apes differ quantitatively, although caution is required here because the studies were not conducted at the same time and in the same place. Orangutans in Danum Valley decrease their fruit-feeding time to less than 50% only infrequently (7 of 27 months (Kanamori *et al.* 2010) and fruit feeding time for gibbons at Tuanan was more than 50% even at the lowest fruit availability (Vogel *et al.* 2009). Red leaf monkeys were apparently less dependent on fruits and seeds. Fruit and seed feeding time was less than 50% for the majority of the study period (16 out of 25 months). During the period of fruit scarcity, red leaf monkeys shifted their diet from fruits and seeds to leaves, while gibbons continue to search for fruits, such as figs. Orangutans are intermediate to these two species.

Fallback foods

Red leaf monkeys in Danum Valley used the young leaves of *Spatholobus macropterus* as a fallback food, as consumption of these leaves was negatively correlated with the availability of preferred foods (Marshall *et al.* 2009). Young leaves of other species were not fallback foods, as their feeding time was not related to fruit availability.

317 Fallback foods can be classified into ‘low-quality’ and ‘high-quality’
318 foods (Lambert 2007), and the fallback strategies of red-leaf monkeys and
319 gibbons seem to rely on ‘low-‘ and ‘high-quality’ foods, respectively. Dependence
320 on ‘low-quality’ foods is often associated with digestive and dental adaptations
321 that allow the extraction of sufficient energy from the low-quality foods (Marshall
322 *et al.* 2009), including the foregut fermentation of red leaf monkeys (Lambert
323 1998). Unlike brachiating gibbons, who can move quickly in the canopy (Vogel *et*
324 *al.* 2009), it is difficult for red leaf monkeys to effectively search for rare
325 resources, such as fruiting fig trees, making abundance a particularly important
326 factor in finding fallback foods in their habitat.
327 Red leaf monkeys appear to depend on young leaves of *S.*
328 *macropterus* as fallback food for two reasons: high protein content and high
329 abundance. There is a universal trend among colobus monkeys to prefer leaves
330 with more protein (Chapman and Chapman 2002; Kar-Gupta and Kumar 1994;
331 Yeager *et al.* 1997), and this includes red leaf monkeys in Sepilok (Davies *et al.*
332 1988). Condensed tannins or other phenolic compounds do not usually affect
333 food selection of colobus monkeys (Chapman and Chapman 2002; Kool 1992;
334 Maisels *et al.* 1994; Mowry *et al.* 1996), in contrast to monogastric primates such
335 as macaques (Hanya *et al.* 2007). *S. macropterus* differed from other
336 protein-rich leaves by its extreme abundance. The stem density of *S.*
337 *macropterus* (302/ha) was much higher than those of other leaf food species
338 (0.25-34/ha). Animals can reduce searching cost by eating abundant species
339 (Hanya *et al.* 2007). This is particularly important for red leaf monkeys, which do
340 not have special adaptations for quick movement through the canopy like
341 gibbons (Vogel *et al.* 2009). Interestingly, the young leaf of *S. macropterus* is

also one of the important fallback foods for sympatric orangutans, constituting more than 20% of their feeding time during periods of fruit scarcity (Kanamori *et al.* 2010). In response to decreased fruit availability, orangutans decrease their feeding time on fruits to less than 20% and shift to eating young leaves and bark (Kanamori *et al.* 2010). They also cannot move as quickly in the canopy as gibbons (Vogel *et al.* 2009) and may select young leaves of *S. macropterus* as fallback foods for a similar reason to that of red leaf monkeys. However, red leaf monkeys in Sepilok consume young leaves of another species of *Spatholobus* (*latistipulus*), but no single species constituted most of the feeding time (Davies *et al.* 1988), unlike *S. macropterus* in the Danum Valley. The selection of fallback food may be strongly affected by the local flora, and it is not consistent within species.

Marshall and Wrangham (2007) defined fallback foods as food that is low-quality but abundant. Our finding that the leaves of this species contain more protein than common species seems to contradict their definition superficially. However, Marshall and Wrangham (2007) used the term ‘low-quality’ only when compared with preferred food items. If we suppose that the quality of young leaves, including *S. macropterus*, is lower than that of fruits and seeds, and red leaf monkeys chose *S. macropterus* among those ‘low-quality’ foods, our finding and their definition do not contradict. However, leaves and seeds, which are the two most important foods for Colobinae (Kirkpatrick 1999), have different nutritional and distribution properties (Janson and Chapman 1999), and so it is difficult to judge which is lower in quality than the other. In fact, another species of colobine (*Trachypithecus francoisi*) shows a positive correlation between the availability and feeding time of young leaves, but this is not the case for fruits

and seeds (Zhou *et al.* 2009). A comprehensive comparison is necessary between these two types of foods in order to evaluate the value as food for colobines.

In conclusion, we found that the red leaf monkey increased seed and whole-fruit consumption in response to the supra-annual increase in fruit availability, which is the essentially the same response as that found in sympatric monogastric primates. However, they depended more on young leaves, in particular *Spatholobus macropterus*, as fallback foods than did gibbons or orangutans. This species appeared to be eaten so often due to its high protein content and extreme abundance.

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Table 1. Number of species consumed by the red leaf monkeys

Food category	No. Species Total	No. Species Tree	No. Species Liana	No. Species Epiphyte
Young leaf	68	50	14	4
Seed	54	40	14	0
Whole fruit	27	21	6	0
Flower, flower bud	11	8	3	0
Pith	4	2	2	0
Bark	5	5	0	0
Mature leaf	1	1	0	0

Table 2. Best-fit generalized linear models for the effect of phenology on the seasonal variations of diet

a. Feeding time of fruits and seeds
QAIC=6.88, R^2=0.35, P=0.00043

	Coefficient	SE	t	p
(Intercept)	0.35	0.06	6.22	0.000
%Fruiting tree	6.90	1.96	3.52	0.002

b. Feeding time of young leaves
QAIC=6.78, R^2=0.33, P=0.00073

	Coefficient	SE	t	p
(Intercept)	0.59	0.05	11.20	0.000
%Fruiting tree	-6.21	1.84	-3.38	0.003

%Fruiting tree: Percentage of trees bearing food fruits or seeds

Table 3. Feeding time of main food species and the months when they were consumed

Category	Species	Family	Time	2006	2007											2008											
				D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Young leaf	*Spatholobus macropterus*	Leguminosae	27.9%	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Seed	*Chionanthus pluriflorus*	Oleaceae	4.2%				*	*	*									*	*	*						*		
Seed	*Nothaphoebe umbelliflora*	Lauraceae	4.1%	*	*	*	*	*				*						*	*				*	*	*	*		
Fruit	*Ficus xylophylla*	Moraceae	2.7%				*										*							*				
Seed	*Syzygium racemosum*	Myrtaceae	2.6%		*	*																						
Seed	*Lithocarpus gracilis*	Fagaceae	2.5%										*	*	*													
Seed	*Paranephelium xestophyllum*	Sapindaceae	2.4%									*	*	*									*	*	*			
Fruit	*Ficus trichocarpa*	Moraceae	2.1%		*						*																*	
Seed	*Spatholobus macropterus*	Leguminosae	2.1%							*	*		*	*	*													
Seed	*Bauhinia* sp1	Leguminosae	2.1%			*	*										*	*	*									
Seed	*Chisocheton sarawakensis*	Meliaceae	1.8%												*							*	*		*	*	*	
Seed	*Litsea elliptibacea*	Lauraceae	1.7%			*	*	*	*	*																*	*	*
Young leaf	*Ziziphus angustifolia*	Rhamnaceae	1.5%			*	*	*		*		*		*	*	*	*	*	*	*	*					*	*	
Seed	*Ardisia elliptica*	Myrsinaceae	1.4%																		*		*					
Seed	*Nephelium cuspidatum*	Sapindaceae	1.2%										*	*	*	*												
Young leaf	*Xanthophyllum affine*	Polygalaceae	1.1%	*			*			*									*							*	*	*
Fruit	*Bridelia pinangensis*	Euphorbiaceae	1.1%		*																							
Seed	*Syzygium rivulare*	Myrtaceae	1.0%										*															

* indicates that the food was eaten in that month.
Only foods which constituted at least 1% of the feeding time during the study period was included.

Table 4. Best-fit models for the effect of leaf chemistry and abundance on young leaf sele

a. Food (1) vs. non-food (0)
AIC=17.6, R^2=0.54, P=0.0001

	Coefficient	SE	t	p
(Intercept)	-9.24	3.80	-2.43	0.015
Crude protein	56.20	23.93	2.35	0.019

b. Feeding time of young leaves
AIC=-79.3, R^2=0.99, P<0.00001

	Coefficient	SE	t	p
(Intercept)	-0.16	0.02	-8.23	0.077
NDF	-0.82	0.05	-16.55	0.04
Crude ash	7.99	0.58	13.75	0.046
Crude lipid	2.29	0.22	10.31	0.062
Condensed tannin	0.07	0.01	9.75	0.065
Abundance	0.00	0.00	18.57	0.034

536

537 Legends for figures

538 Fig. 1. Climate data from the Danum Valley Field Centre for December
539 2006-December 2008.

540 Fig. 2. Fruiting (a) and flushing (b) phenology between July 2004 and December
541 2008. Values are percentage of total trees in the sample plot bearing fruit
542 at a given time. Closed diamonds: all trees; open squares: red leaf
543 monkey food species only.

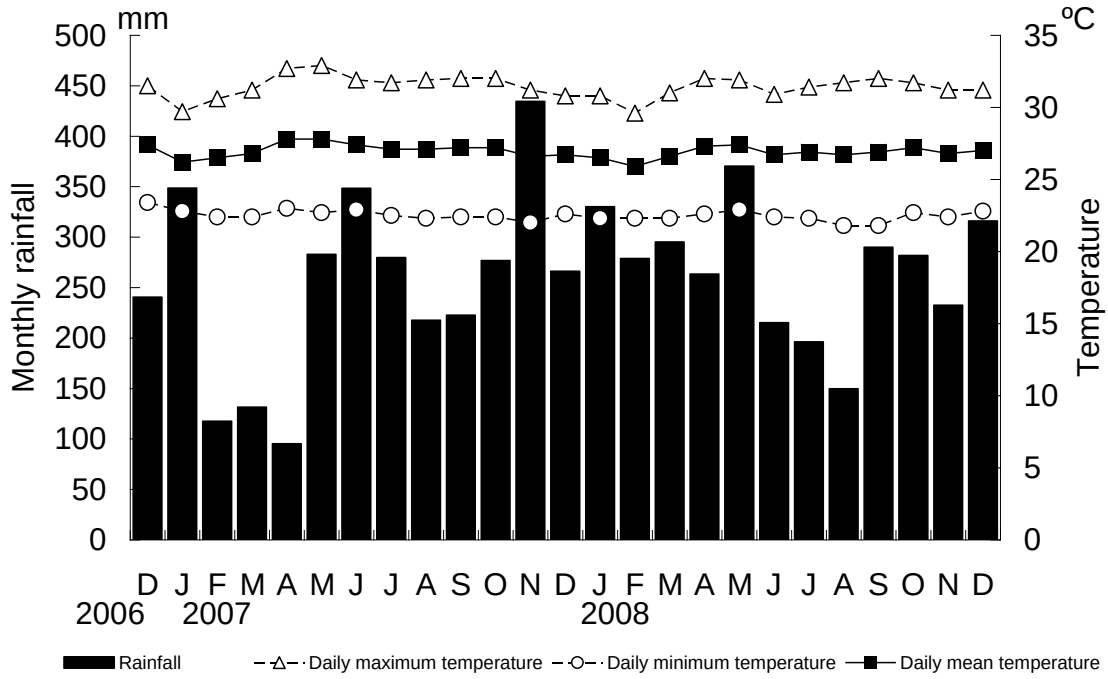
544 Fig. 3. Seasonal changes in the diet composition of red leaf monkeys; values are
545 percent of monthly feeding time spent on each food category.

546 Fig. 4. Relationships between fruiting phenology (proportion of trees bearing
547 fruits in the phenology plot) and time spent feeding on (a) fruits and seeds
548 and (b) young leaves.

549 Fig. 5. Relationships between flushing phenology (proportion of trees having
550 young leaves in the phenology plot) and time spent feeding on (a) fruits
551 and seeds and (b) young leaves.

552 Fig. 6. Comparison of chemical properties and abundance between consumed
553 and non-consumed young leaves (mean+SD) Values are proportion of
554 dry weight for (a)-(d). Consumed species include *Spatholobus*
555 *macropterus* (Leguminosae; 27.9% of feeding time), *Ziziphus angustifolia*
556 (Rhamnaceae; 1.5%), *Xanthophyllum affine* (Polygalaceae; 1.1%),
557 *Ryparosa hullettii* (Flacourtiaceae; 0.5%), *Parashorea malaanonan*
558 (Dipterocarpaceae; 0.2%), *Koompassia excelsa* (Leguminosae; 0.1%),
559 and *Nothaphoebe umbelliflora* (Lauraceae; 0.1%).

560



561

562 Fig. 1

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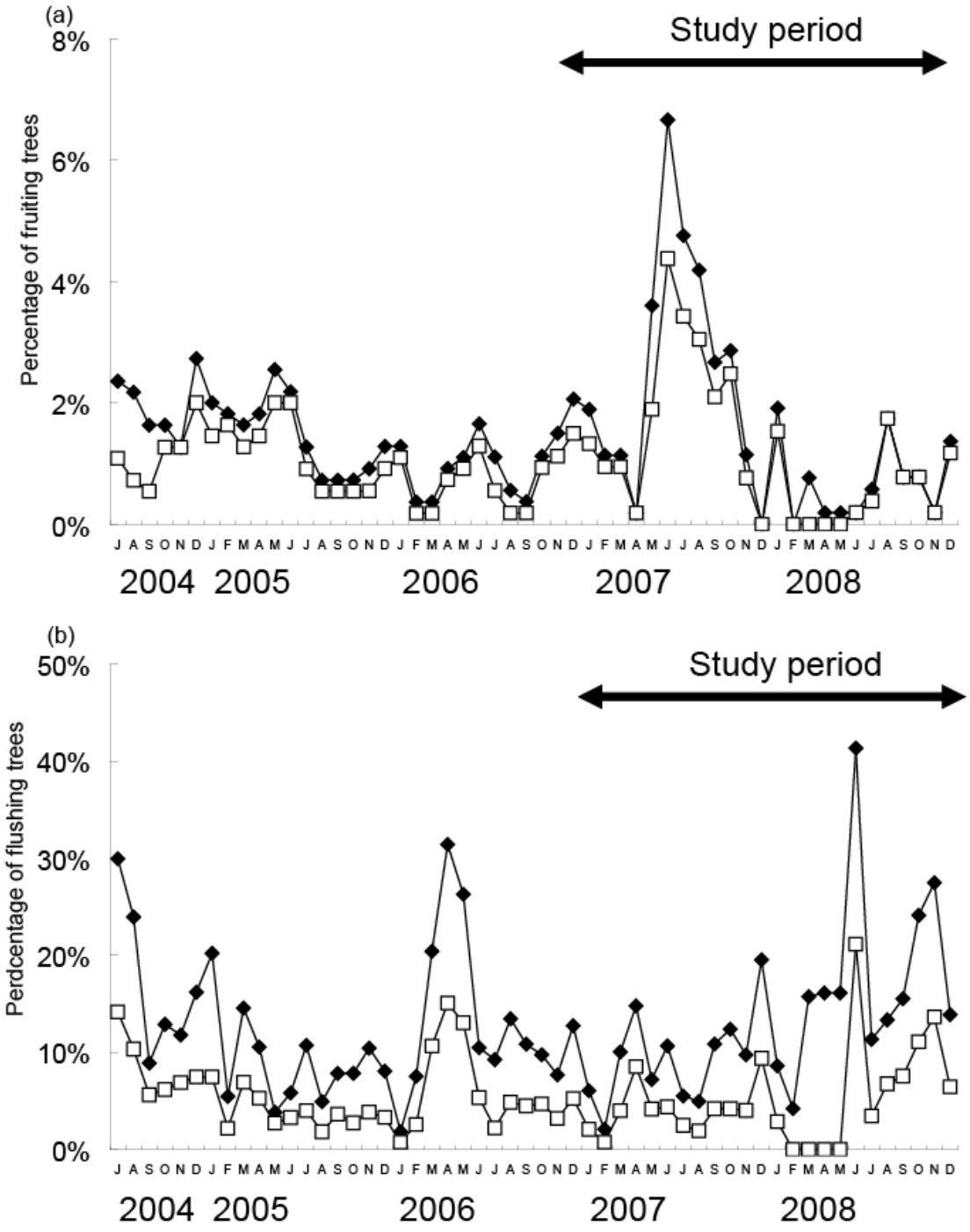

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565 Fig. 2

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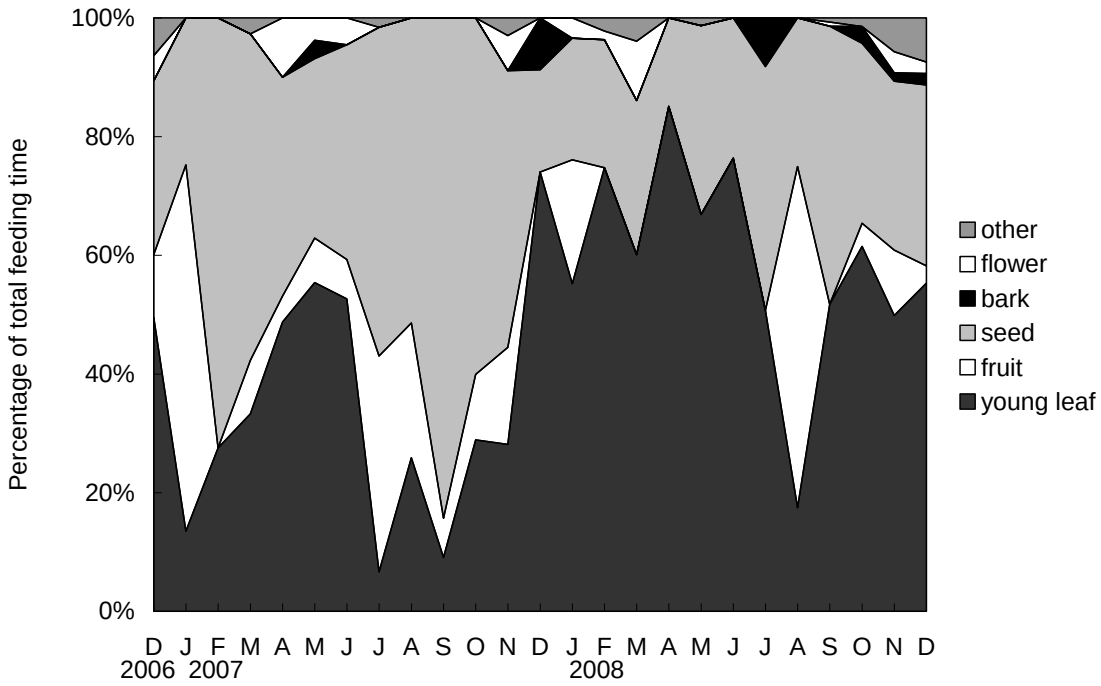

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568 Fig. 3

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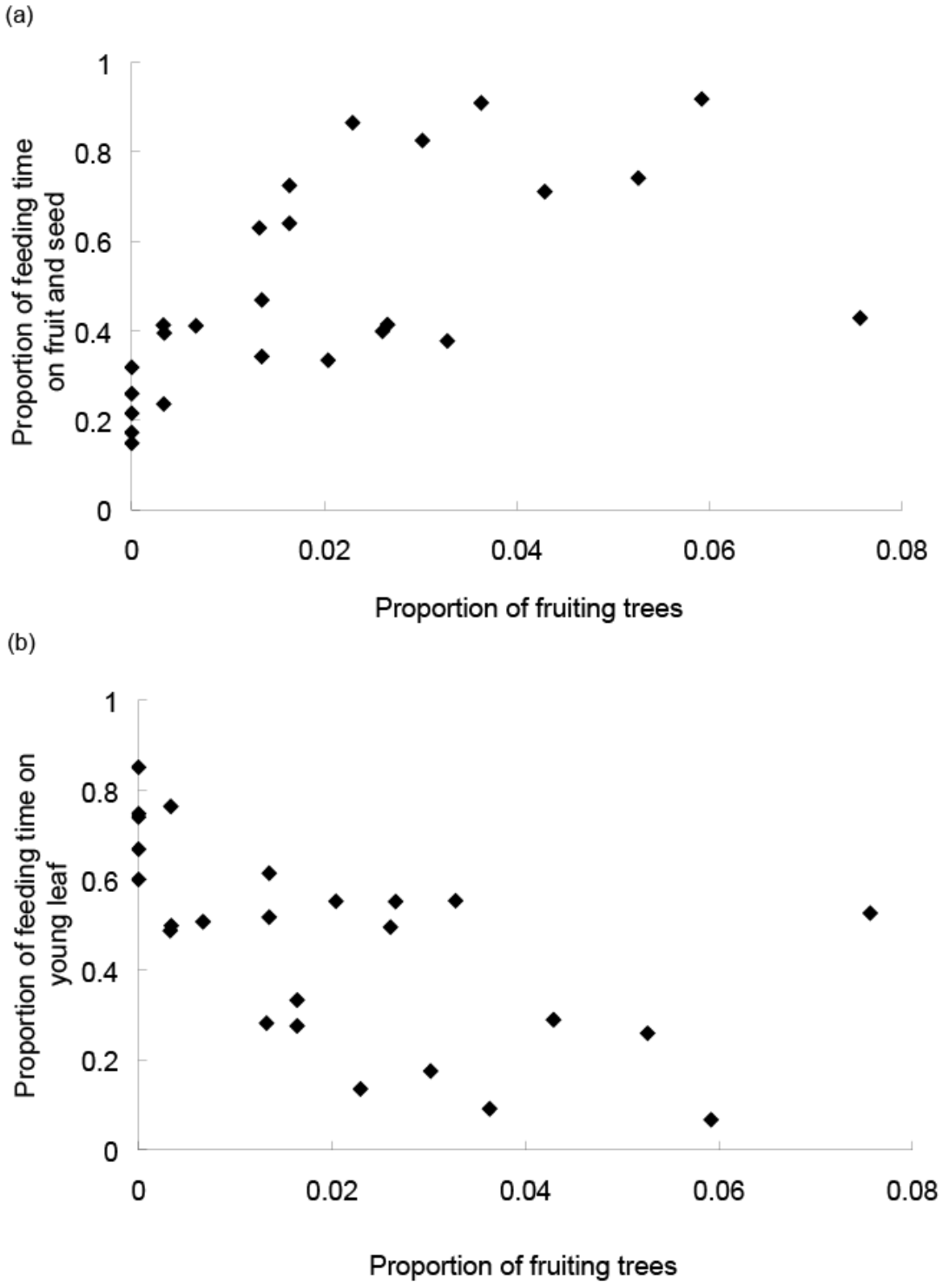

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571 Fig. 4

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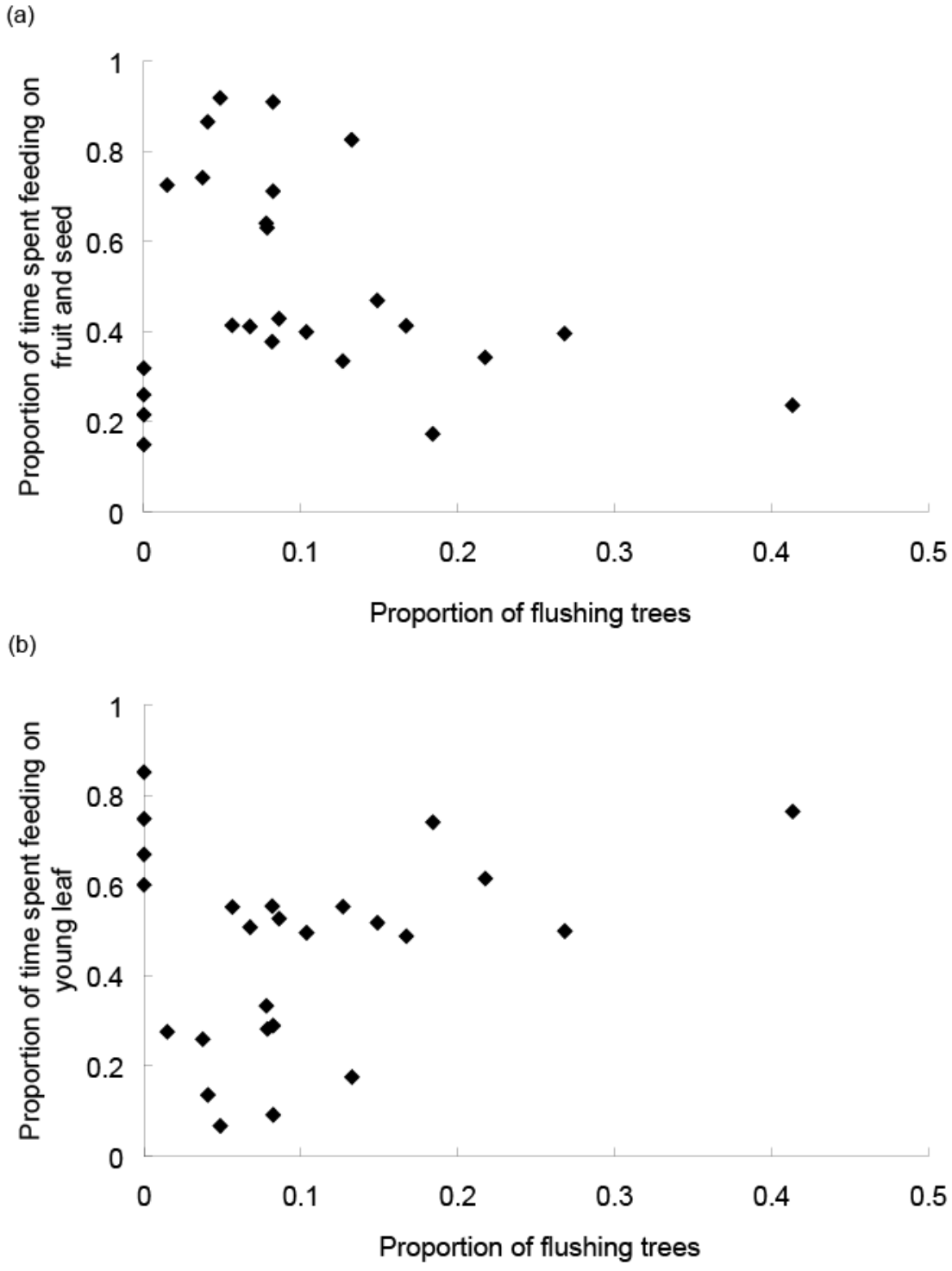

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574 Fig. 5

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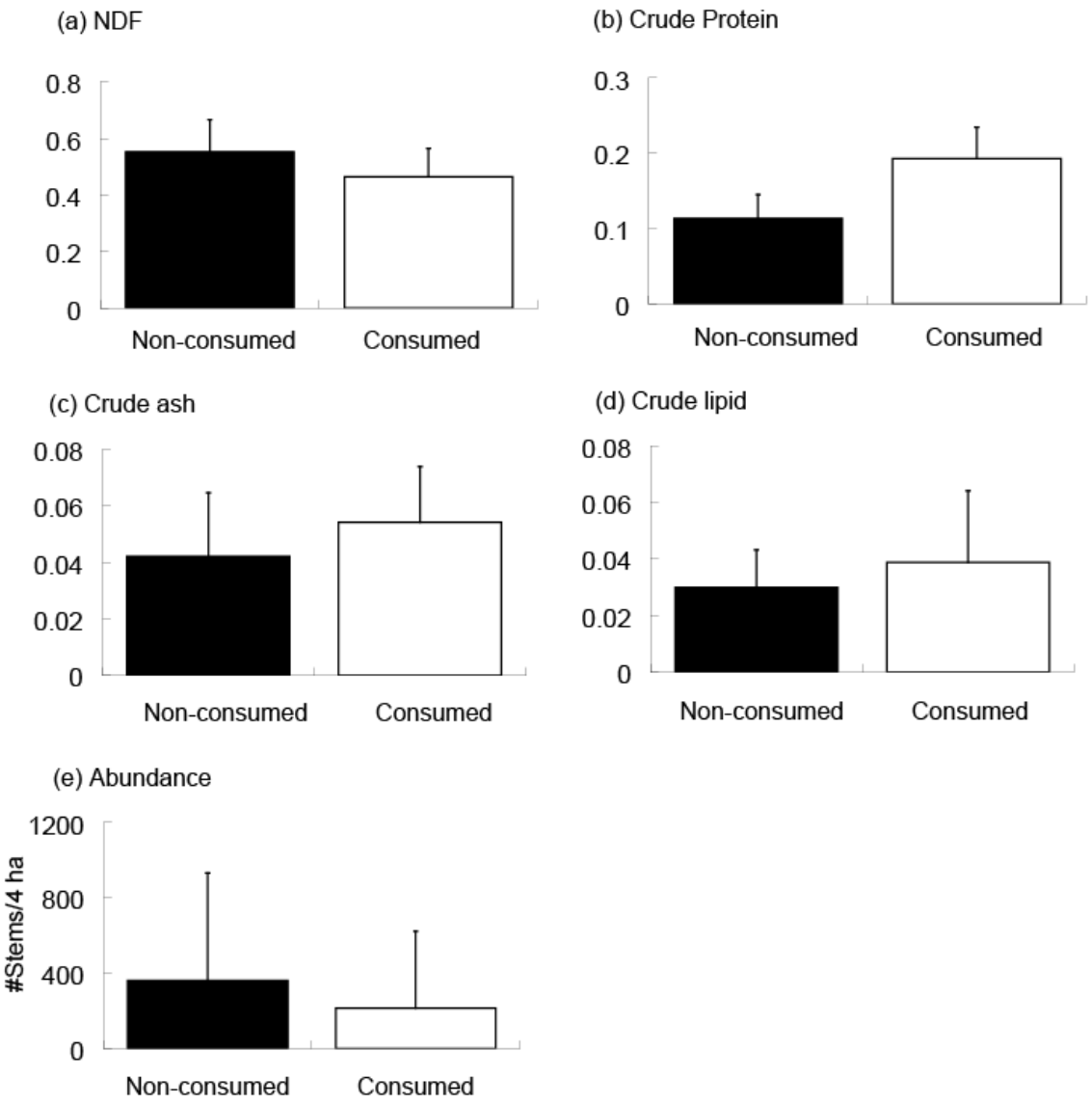

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577 Fig. 6